Truncation Points for Selection in a Population with Overlapping Generations

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(Received April 20, 1992)

Abstract Simple procedures for computing the truncation points of selection such as (1) predicted genetic values on truncation points and (2) average genetic values of selected parents should be on the same level for each age class of parents in a population with overlapping generations, are presented. To illustrate these procedures, the path of bulls' dams in a dairy cattle population was taken as a choice for a numerical example. The results were compared with two other selection methods, intra-age selection and selection on common truncation point on phenotypic values to assess their practicability in optimizing the age structure and prediction of genetic response to truncation selection. The problems in pursuing such selection policies are also discussed.

Anim. Sci. Technol. (Jpn.) 63 (11) : 1109-1114, 1992

Key words : truncation points, selection across age classes, age structure

In a livestock population with overlapping generations, the optimum breeding policy is based on the best combination of selected proportions within and across age classes. Inter-age class selection affects the age structure of parents which determines the generation interval and reflects on the rate of genetic improvement. HILL^{8,9)} developed a formal matrix method to predict and compare the genetic responses to selection for the short and long term improvement breeding plans with fixed age structure of parents in a population with overlapping generations and sub-groups. HOPKINS and JAMES^{10,11)} demonstrated the recurrence relationship to relate the breeding values of age-sex classes from different time periods which imply the effect of age structure and initial genetic differences between age groups. It has been pointed out that the methods are not suitable for predicting the response to selection with optimal generation intervals¹³⁾, since the generation interval is a

fixed input parameter of these models. The optimum age structure is required to construct an optimum breeding plan. RICHARD *et al.*¹⁾ considered the fact that when genetic gains are being made in a population where generations overlap, progeny of younger parents will, on average, be genetically superior to progeny of older parents. Further, the rate of gain can be increased by making allowances for the genetic effects of parental age. They concluded this while comparing the following three selection criteria : 1) selection on the deviation from the means of each parental age class, 2) at common truncation point on phenotypic values, and 3) at the truncation point on the same predicted breeding value. They found the truncation point by trial and error using the Table of probits proposed by FISHER and YATES⁶⁾. However, they did not present the systematic methodology which could be combined in a computing program. DUCROCQ and QUAAAS⁵⁾ presented an algorithm for determining the

truncation point following the optimal rule proposed by BICHARD *et al.*¹⁾ using Newton's method⁴⁾. This algorithm coincides with the second method of BICHARD *et al.*¹⁾.

The main objective of this study, is to extend their algorithm to calculate the truncation point of selection for the third method and a 'new' truncation point which takes account the distribution of selected parents from different age classes, at the same average genetic merits. The procedures are also applied to decide an optimal proportion of parents selected across age subgroups or introduced from an exotic population.

Materials and Methods

Methods of selection : Four methods of selection differentiated by the truncation point of selection among age classes were settled, including the three methods of BICHARD *et al.*¹⁾, as :

- (1) selection of fixed proportion within age classes : Method I,
- (2) selection at the common truncation point on phenotypic value or selection index predictor of breeding value : Method II,
- (3) selection at each truncation point on the same predicted genetic value : Method III, and
- (4) selection at each truncation point with the same average genetic values of selected parents : Method IV.

General formulae : Average genetic merit of the selected parents over the candidates for selection is expressed as :

$$g = Ir\sigma_A \quad (1)$$

where r refers to accuracy of selection, σ_A to genetic standard deviation and I to selection intensity. Under the assumption of normal distribution ($N(0, \sigma^2)$)

$$I = f(k)/F(k) \quad (2)$$

where,

$f(k)$ refers to the density at k in a normal distribution :

$$f(k) = \exp[-k^2/(2\sigma^2)]/(\sqrt{2\pi}\sigma) \quad (3)$$

$$F(k) = \int_k^\infty f(x) dx \quad (4)$$

Calculation of truncation point for selection :

If a genetic trend exists in the population with overlapping generations and the accuracy of selection increases as candidate gets older, animals of different age classes come from the distribution with different means and variances. It assumed that all animals are kept from one year to another except for accidental reasons. Selection is usually performed by truncation within or across age classes. Truncation points may be unique over all age classes or different among age classes, depending upon the selection objectives. The unit of measurements, the genetic standard deviation, was assumed to be constant over all age classes. Additive genetic values and its selection index predictor are normally distributed with $N(m_i, 1)$ and $N(m_i, 1/r_i^2)$ for the i -th age class respectively, where m_i refers to the average genetic values of the i -th age before selection and r_i to the accuracy of selection.

Method I : For Method I, the proportions of selected parents among age classes were identical to the distribution of candidates and the selection intensity may be computed according to BURROWS²⁾.

Method II : When parents are selected at the common truncation point K , the overall selected proportion (P) is

$$P = \sum q_i F[(K - m_i) r_i] \quad (5)$$

DUCROCQ and QUAAS⁴⁾ solved this nonlinear equation iteratively for K using Newton's method⁴⁾ as described below. The deviation of calculated proportion from a given proportion (P^*) is

$$d(K) = P - P^* \quad (6)$$

To get K such that $d(K)=0$, start with some prior value K_0 , e.g. K_0 = means of the youngest age class, and iterate on :

$$K_{n+1} = K_n - d(K_n)/d'(K_n) \quad (7)$$

where

$$d'(K_n) = - \sum q_i r_i f[(K_n - m_i) r_i] \quad (8)$$

Once K is obtained, other relevant quantities

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are calculated. The proportion of the parents selected from the i -th age class (p_i) to total number of selected parents is

$$p_i = (q_i/P^*) F[(K - m_i) r_i] \quad (9)$$

Average genetic superiority of the parents (Δg) selected across age classes as the deviation from the mean of the youngest age (m_c : subscript c refer to the youngest age class) is

$$\Delta g = \sum p_i \{r_i f[(K - m_i) r_i] / F[(K - m_i) r_i] + m_i - m_c\} \quad (10)$$

In this case, truncation point is common to all age classes.

Method III: Assuming the highest genetic means for the youngest age class and the truncation point for this class as K_c (Fig. 1), then, the genetic values of animals at K_c in the i -th age class are $m_i + (K_c - m_i) r_i^2$ and the truncation point (K_i) where animals in the i -th age class should have the same genetic values as animals at K_c in the youngest age is

$$K_i = [(m_c - m_i) + (K_c - m_c) r_c^2 + m_i r_i^2] / r_i^2 \quad (11)$$

When the accuracy of selection is same among age classes ($r_c = r_i$), marginal deviation ($K_i - K_c$) at the same predicted genetic values is

$$K_c - K_i = (m_i - m_c) (1 - r_c^2) / r_c^2$$

which coincided with equation (2) of BICHARD *et al.*¹¹. The equations (5) to (10) are modified by transferring K to the truncation point for each age class (K_i) as:

$$P = \sum q_i F[(K_i - m_i) r_i] \quad (5.1)$$

$$h(K) = P - P^* \quad (6.1)$$

$$K_{c,n+1} = K_{c,n} - h(K_n) / h'(K_n) \quad (7.1)$$

$$h'(K_n) = -\sum q_i r_i f[(K_{i,n} - m_i) r_i] \quad (8.1)$$

$$p_i = (q_i/P^*) F[(K_i - m_i) r_i] \quad (9.1)$$

$$\Delta g = \sum p_i \{r_i f[(K_i - m_i) r_i] / F[(K_i - m_i) r_i] + m_i - m_c\} \quad (10.1)$$

Combining the equation (11) with (6.1) to (8.1), K_c can be computed such that $h(K)=0$, and thus K_i is calculated from equation (11).

Method IV: Again, when the truncation point of selection for the youngest age class is K_c , the selection intensity (I_c) is calculated from equation (2). The standardized selection differentials (selection intensity (I_i^*)), in which

Fig. 1. Illustration of the symbols and distribution of different parental age classes with overlapping generations. m = genetic means, K = truncation point, $\bar{x}$ = means of selected parent.

the average genetic values of selected parents in the i -th age class are on the matching level of the average in the youngest age class, are

$$I_i^* = (m_c - m_i + r_c I_c) / r_i \quad (12)$$

Truncation point (K) with a given I^* can be computed using Newton's Method³¹. From equation (2),

$$I = f[(K - m) r] / F[(K - m) r] \quad (13)$$

The deviation of calculated I from a given I^* is,

$$e(K) = I - I^* \quad (14)$$

$$K_{n+1} = K_n - e(K_n) / e'(K_n) \quad (15)$$

where,

$$e'(K_n) = I_n [I_n - (K_n - m) r], \quad (16)$$

$e'(K_n)$ is the rate of change in I at K_n . The $e'(K_n)$ can be obtained by differentiating the equation (13) with a given K_n . Thus, the

truncation point for each age class (K_i) for a given I_i^* based on K_c can be obtained such that $e(K)=0$. Combining the equations (12) to (16) with (6.1) to (8.1) and asymptotically approximating K_c to the optimum value with the condition of equation (12), optimal truncation point for each age class can be obtained iteratively.

Since the size of the actual animal population is not infinite, actual selection intensity (I) in equations (10) and (10.1) should be

recalculated according to BURROWS²⁾.

Results and Discussion

Since the path of bull's dams has many age classes, and older cows have a higher accuracy of selection, the algorithms proposed were applied to this path to illustrate the merit of its application. Main parameters used are listed in the upper 4 lines of Table 1. A unique trait of interest for selection was assumed to be milk production. The genetic differences

Table 1. Comparison of different selection criteria on age structure, truncation point of selection and genetic superiorities.

		Age classes (years)					
		3	4	5	6	7	8
Means of age classes (m_i) ^{a)}		0.500	0.400	0.300	0.200	0.100	0.000
Accuracy of selection (r_i)		0.500	0.600	0.645	0.670	0.690	0.710
Proportions among classes		0.271	0.217	0.174	0.139	0.111	0.089
No. of candidates (total nos. 2,500)		677	541	433	347	277	222
Proportions of selected parents							
Method I ^{b)}	5.87 ^{c)}	0.271	0.217	0.174	0.139	0.111	0.089
Method II	5.43	0.371	0.236	0.159	0.109	0.075	0.050
Method III	5.51	0.332	0.249	0.173	0.117	0.078	0.052
Method IV	5.60	0.293	0.260	0.186	0.125	0.082	0.054
Truncation points ^{a)}							
Method I		1.68	1.30	1.10	0.96	0.82	0.69
Method II		1.20	1.20	1.20	1.20	1.20	1.20
Method III		1.38	1.14	1.11	1.14	1.16	1.18
Method IV		1.57	1.08	1.03	1.07	1.12	1.14
Predicted genetic values on truncation points ^{a), d)}							
Method I		0.621	0.405	0.343	0.264	0.181	0.097
Method II		0.300	0.369	0.383	0.374	0.363	0.358
Method III		0.345	0.345	0.345	0.345	0.345	0.345
Method IV		0.392	0.324	0.310	0.315	0.322	0.327
Genetic superiorities ^{a)}							
Method I	0.665 ^{e)}	0.699	0.738	0.701	0.635	0.563	0.490
Method II	0.676	0.607	0.710	0.732	0.722	0.706	0.695
Method III	0.677	0.641	0.692	0.702	0.699	0.692	0.685
Method IV	0.676	0.677	0.676	0.676	0.675	0.673	0.671

a) in genetic s.d. units.

b) Methods refer to text.

c) generation intervals as average ages of selected parents.

d) as the deviation from the means of age class 3.

e) average genetic superiorities as deviation from the means of age 3.

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between consecutive age classes were assumed to be 0.1 genetic standard deviation (75 kg), based on the actual yearly improvement in dairy cattle population in Hokkaido¹⁴⁾, considering phenotypic standard deviation of 1,500 kg and heritability of 0.25. The accuracies of selection were the rounded values based on an increase in a number of lactation records with older cows. The rate of selection was 500 cows from 2500 candidates. The assumed proportions of candidates among the age classes were relative proportions assuming their stayability to be 0.80. Initial point of selection ($K_{c,0}$) was settled on the means of the youngest age class. The limited deviation of truncation points ($d(K)$, $h(K)$) and selection intensity ($e(K)$) at their convergence were settled to be 10^{-5} in equations (6), (6.1) and (14) respectively.

Under these conditions, the truncation point with a given selection intensity (Method IV) was obtained in less than 4 cycles. When the deviation of selected proportion converged to the limited threshold range, the number of iterations were 3 for Method II and 9 for both Methods III and IV. When there were some differences in accuracy of selection among age classes, as in numerical example, the number of cycles required for the convergence increased.

The comparison of calculated age structures, truncation point and genetic selection differentials with 4 selection criteria, is presented in Table 1. When parents were selected according to Method II, the generation interval was the shortest of four methods ascribed to the higher proportion of selection from younger parents, followed by Method III and IV. However, the average genetic superiorities were highest for Method III followed by Method IV and II, though the differences among these three methods were very small. Age structures of parents (*e.g.* generation interval) and estimated genetic superiorities depend on the methods of selection applied. These quantities would also be affected by the number of age classes,

genetic difference among age classes and the accuracy of selection. More work would be needed to determine an optimal method among those examined in this study with combinations of different genetic and population parameters.

Cows not selected as parents, in this model, were never used for breeding but were kept from one year to another for possible future use. In practice, breeder would be reluctant to pursue such a policy as already described by JAMES¹²⁾ and HILL⁹⁾. The results achieved here have some similarity with COCHRAN³⁾ and HOPKINS and JAMES^{10,11)}. The distribution of actual dairy population of each age class would be skew due to earlier culling of low producers. In principle, the methods proposed in this paper would not be suitable for application to such a skewed population due to an implicit assumption of normal distribution. However, it may be of some interest to combine with HENDERSON'S¹²⁾ BLUP method to predict breeding values.

Acknowledgments

The authors acknowledge Dr. N. NOGUCHI, Department of Agricultural Engineering, for his valuable suggestions on computational procedures. The results of this study were computed at the Hokkaido University Computing Center.

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世代重複集団における選抜切断点の演算法

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複数の年齢群を含む世代重複集団について, (1) 各年齢群の選抜切断点が期待遺伝的能力値で等しい選抜, (2) 各年齢群から選抜された種畜の平均期待遺伝的能力値が等しくなる選抜, を実施するときの切断点を Newton 法で算出する方法を提示した. 種雄牛母牛の選抜を数値例として, 候補畜と同じ比率で選抜する年齢群内選抜と表型値ないしは選抜指標値で全年齢群に共通な切断点での選抜を含め, これら4方法の選抜の実施した時の選抜種畜の理論的な年齢構成, 選抜切断点, 遺伝的選抜差を示し, 本方法の適用性について考察した.

日畜会報, 63 (11): 1109-1114, 1992